

Reproductive and physiological consequences of egg predation  
for glaucous-winged gulls

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**Abstract**

Reproductive and physiological consequences of egg predation  
for glaucous-winged gulls

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In this study, I examined the effects of egg loss on reproductive and physiological responses of glaucous-winged gulls (*Larus glaucescens*). Gull eggs at South Marble Island, Glacier Bay, Alaska, are subject to harvesting by native peoples and predation by bald eagles (*Haliaeetus leucocephalus*). I monitored egg-laying and hatching success within the context of natural predation and annual variability. Eagle predation occurred through the incubation period in 1999, but was concentrated in the mid-incubation period in 2000. Early lay dates and young clutches at the time of predation best predicted whether gulls renested in 1999, whereas the date of predation best explained whether gulls renested in 2000.

I conducted egg-removal experiments in both years to test the effects of the timing of egg-removal on the timing and number of replacement eggs. Most (95%) gulls from nests from which I removed the first egg continued to lay 1 to 3 more eggs. Pairs with their first egg removed laid on average 1.24 (in 1999) and 1.06 (in 2000) more eggs than those in the unmanipulated group, but there was no difference in the number of

eggs that hatched. Pairs replaced their clutches that I removed with another 3-egg clutch in 82% of the cases. Those pairs laid on average 2.71 (in 1999) and 2.01 (in 2000) more eggs than those in the unmanipulated group, but there was no difference in the number of eggs that hatched.

I looked for physiological effects of laying replacement clutches by comparing (1) body condition, (2) baseline corticosterone levels, and (3) stress-induced corticosterone levels between gulls that had incubated to hatching three eggs, either from the original or a replacement clutch. I found neither body condition or baseline corticosterone levels to differ between groups. However, I found evidence of stress response modulation in females that had laid a replacement clutch. I suggest that suppression of this stress response may be evolutionarily advantageous to females by allowing them to continue breeding activities and thereby not reducing their hatching success. Lastly, I discuss the potential future impacts of harvesting at the individual and colony level and propose management guidelines.

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## INTRODUCTION

Seabird populations are regulated by intrinsic demographic factors such as rates of adult and juvenile survivorship, production of young, and/or recruitment of juveniles into the breeding population (Newton 1998). Productivity is determined by clutch size and the success of maintaining clutches until chicks fledge. One major extrinsic influence on productivity is predation on eggs. In this study, I examined the effects of egg loss on reproductive and physiological responses of glaucous-winged gulls (*Larus glaucescens*).

Egg predation in gulls can cause near or complete reproductive failure (Spear and Anderson 1989, Ewins 1991, Vermeer et al. 1991) and influence nesting densities (Southern et al. 1985, Spear and Anderson 1989). Egg predation by one predator species, such as humans or bald eagles, can facilitate predation by conspecifics (Good et al. 2000; Hand 1980). Documented glaucous-winged gull egg predators include conspecifics (Verbeek 1988, Good et al. 2000), common ravens (*Corvus corax*) (Patten 1974), American crows (*Corvus brachyrhynchos*) (Verbeek 1988), bald eagles (*Haliaeetus leucocephalus*) (Good et al. 2000; Thompson 1989), and humans (Vermeer et al. 1991).

Predation on eggs results in egg loss and creates the need to replace eggs.

Replacement laying has been documented in seabirds that lay single-egg clutches as well as multi-egg clutches (Parsons 1976, Hipfner et al. 1999). Replacement laying is common in ground nesting gulls, which have evolved to replace clutches lost to factors such as floods and weather, as well as to predators (Brown & Morris 1996). The ability to replace clutches may be influenced by seasonal effects (Parsons 1976; Wendeln et al. 2000), breeding experience (Wooler 1980), food availability (Pierotti & Bellrose 1986), and the age of the lost clutch (Parsons 1975, 1976, Wooler 1980). The resulting replacement eggs change in composition and size during protracted laying (Parsons 1976), which may negatively affect chick-survival (Nager et al. 2000). The long-term costs and benefits of renesting on longevity and lifetime reproductive success are not well understood (Brown & Morris 1996).

Large gulls of the genus *Larus* are indeterminate layers (Parsons 1976). Following the loss of all eggs in the nest prior to clutch completion, most individuals continue to lay until their clutch contains a common number of eggs. In glaucous-winged gulls, egg laying typically occurs at the rate of 1 laid every 2 days and terminates when the nests contains three eggs. When not interrupted, the incubation period of the last-laid egg is about 27 days (Verbeek 1993). The onset of incubation has been shown to cause complete degeneration of the fourth follicle in the closely related herring gull (*Larus argentatus*) (Parsons 1976). Intermittent incubation during the laying period delays follicular atresia, which allows follicles to be available for rapid development if egg

replacement is needed (Wooler 1980). Replacing a clutch after the onset of incubation requires time to resume follicle growth.

There are additional direct and indirect short-term costs associated with laying replacement eggs. Egg production is energetically costly for females (Monaghan & Nager 1997). Females must have sufficient calcium, lipid and protein resources to produce eggs (Walsberg 1983). These resources come from stored reserves and increased food intake (Walsberg 1983). Egg laying can also incur costs in males. In glaucous-winged gulls, males provide supplementary food to their mates before and during the laying period. When laying replacement eggs becomes necessary, males must extend this provisioning period (Salzer and Larkin 1990, Mawhinney et al. 1999). Increasing food intake for females through self-feeding and male provisioning requires increased foraging effort, which may indirectly reduce fitness and effect physiological stress (Kitaysky et al. 1999).

The costs of energetically demanding processes such as egg laying and chick-rearing have been examined in several ways. Costs have been measured indirectly through poorer quality eggs or chicks (Monaghan 1998, Nager et al. 2000), reduced productivity rates (Risch & Rohwer 2000), and reduced post-fledging chick survival. Costs have also been measured directly through physiological measures such as body condition (Reid 1987; Wendeln et al. 2000) and metabolic rates (Ward 1996).

Measures of the glucocorticosteroid corticosterone may provide additional insight into physiological response to increasing reproductive demands. Corticosterone has been examined in birds in relation to unpredictable environmental conditions such as food shortages (Kitaysky et al. 1999) and predictable life-history events such as breeding (Wingfield et al. 1995). Corticosterone is secreted in birds in response to stressful events and regulates body maintenance processes by modifying behavior (Kitaysky et al. 1999). Elevated levels of corticosterone can result in behavior, such as abandonment of breeding, which promotes self-maintenance at the expense of reproductive effort. Life-history theory predicts that short-lived birds should maximize current reproduction, whereas long-lived birds should maximize future reproduction (Stearns 1992). However, a recent study has shown that long-lived black-legged kittiwakes (*Rissa tridactyla*) can suppress their stress responses, presumably to increase reproductive success, in moderately unfavorable conditions (Kitaysky et al. 1999).

The goal of this study was to better understand the effects of egg loss at a glaucous-winged gull colony in southeastern Alaska that is subject to harvesting by humans and predation by avian predators. Gull eggs at this colony have been traditionally harvested for human consumption by native peoples; eggs at this colony are also lost in great numbers to avian predators. My objectives were to assess the factors affecting re-laying attempts after egg loss and to investigate the physiological costs to individual gulls for laying replacement eggs. I monitored egg-laying and hatching

success within the context of natural predation and annual variability. I conducted egg-removal experiments to test the effects of the timing of egg-removal on the timing and number of replacement eggs. I looked for physiological effects of laying and incubating replacement clutches. Lastly, I discuss the potential future impacts of harvesting at the individual and colony level and propose management guidelines.

## METHODS

### Study area

I conducted this study in 1999 and 2000 on South Marble Island in Glacier Bay National Park, Alaska (58°39'N 136°0'W)(Figure 1). South Marble Island is located in the central portion of Glacier Bay, which is a recently deglaciated fiord approximately 100 km long and 20 km wide. The 1.5 km<sup>2</sup> island has been exposed from glacial ice for 170-200 years. During this time, vegetation has grown over most of the limestone substrate. Dense spruce (*Picea sitchensis*) forest currently dominates the western half of the island. Grassy rounded hilltops and steeply sloped cliffs characterize the eastern half. Approximately 700 glaucous winged gulls (*Larus glaucescens*) nest on most of the unforested areas. The earliest documentation of the gull colony is from 1941 when an estimated 100 pairs nested on the island (Jewett 1942). Estimates from the 1970's suggest a population of 500-1000 birds (Patten 1974).

### Monitoring eggs and nests

I monitored accessible nesting areas from pre-laying (mid May) through hatching (late July). In both years gulls were defending territories and had begun constructing nests before our arrival. I walked through the nesting areas every 1 – 2 days during the laying period and recorded the appearance of nest structures and eggs. The gulls either flew overhead or stood away from their nests during my presence in the nesting areas.

I checked most nests between 0900 and 2000. Access to half of the nesting areas were limited by tides in 1999, so the timing of nest checks ranged from 0500 to 2300. A small boat allowed regular access to these nests in 2000.

I considered an egg to have been laid on the date observed if I observed no egg in the nest on the day before. I numbered eggs found in sequence and gave alphabetic codes to eggs for which I did not know the exact laying sequence. I excluded from analyses involving lay dates those nests in which lay dates of the first eggs were unknown. To separate renesting attempts from protracted laying, I considered eggs laid  $\geq 9$  days apart to be in separate clutches. I defined lay date of the clutch as the day the first egg was laid and clutch age as the number of days from when the last egg was laid. For analyses, I assumed incubation began on the day the last egg in the clutch was laid. I measured length (L) and breadth (B) of each egg to the nearest 0.1 mm using vernier calipers. To calculate egg volume I used the equation:

$$V = 4.76 \times 10^{-4} \cdot L \cdot B^2$$

after Reid (1987) and Verbeek and Richardson (1982).

#### Factors affecting renesting

I used logistic regression with backward stepwise selection to test if the probability of renesting after predation was influenced by lay date and age of the clutch at predation. Because predation date is the sum of lay date and age of clutch at predation, I could

not test the three factors together. Terms were evaluated for removal based on the likelihood-ratio statistics of the resulting models with one of each terms removed. The term from the model with the largest p-value over 0.10 was removed. The resulting model statistics were then recalculated to see if any other terms were eligible for removal. Removal testing ended when no other terms were eligible for removal. I did not present well-fitting models that include an interaction without both factors that comprise the interaction because those models do not obey marginality restrictions (Venables & Ripley 1999).

#### Nest manipulations

To examine the effects of a controlled egg harvest, I randomly assigned nests to one of three treatments. For the first treatment, I removed the first egg from a nest on the day it was laid ( $n = 14$  in 1999,  $n = 25$  in 2000). For the second treatment, I removed the clutch of three eggs on the day the third egg was laid ( $n = 17$  in 1999,  $n = 24$  in 2000). I removed no eggs from all other nests ( $n = 151$  in 1999,  $n = 140$  in 2000). Many pairs that lost eggs from their first clutch from natural predation (57%) and our manipulations (64%) re-laid eggs in different nest structures. I assumed these “new” nests to belong to the same pair based on proximity to the original nest (i.e., within their defended territory) and egg-laying sequence (Nager et al. 2000). I measured the distances between these nests when possible without causing excessive disturbance.

When neighboring pairs lost and re-laid eggs simultaneously and associations were questionable, those nests were deleted from analyses.

I monitored all eggs every 1 – 4 days until they hatched, disappeared, failed to hatch, or were depredated. I determined the total number of eggs laid and hatched by unmanipulated and manipulated pairs. Because all gulls responded similarly to my presence in the colony, it is unlikely that manipulated and unmanipulated pairs became differentially habituated to my activities. I presented the results with data from each year combined when annual differences were not significant.

#### Physiological effects of laying replacement eggs

To determine whether there were measurable physiological effects on the individuals that had to re-lay a clutch, I compared body condition and corticosterone levels between two subgroups of gulls that I captured. Gulls in the original-clutch group were from pairs that laid 3 eggs and hatched 3 chicks ( $n = 10$  birds). Gulls in the replacement-clutch group were from pairs that laid 6 eggs (re-laid a clutch of 3 after I collected the first clutch) and hatched 3 chicks ( $n = 8$  birds).

To control for breeding stage, I captured adults at the end of their incubation period (0-7 days from hatching dates) using wire mesh cage traps with one-way entry doors staked over the nests. Gulls entered the cages after I left the nesting areas and became trapped when trying to escape as I returned. I usually caught one bird per nest; at 2

nests I caught both adults sequentially ( $n = 83$  birds total). I weighed each bird to the nearest 10 grams with a spring balance, and I recorded four measures of structural size: (i) tarsus, (ii) flattened wing length, from the wrist to the tip of the longest primary (iii) culmen, and (iv) head and bill length, from the tip of the bill to the back of the skull. I took all measurements to the nearest 0.1 mm with calipers, except wing length, which I measured to the nearest 1 mm with a ruler.

I collected blood samples by puncturing veins in the wing or webbing of the feet with disposable syringe needles and collecting blood in heparinized microhematocrit capillary 100  $\mu$ l tubes. I collected the first sample within 3 minutes of capture, defined as the moment when the bird began to struggle to escape from the nest trap. Further samples were collected at 10, 30, and 50 minutes after capture. The hematocrit tubes were emptied into 0.5 ml vials, which were stored on ice. The blood samples were centrifuged and the plasma was separated and frozen within 24 hours of collection. Samples were analyzed for corticosterone levels by radioimmunoassay at the University of Washington (Wingfield & Farner 1975) (Wingfield et al. 1992). The sex of the birds was determined by DNA extracted from the blood samples. Samples were treated with chelax to bind heparin and run through a PCR to amplify the DNA. When results were unclear, the samples were run through pheno-choloroform DNA purification method and re-amplified (for details of methodology see D. Wisti-Peterson *et al. in prep*).

## Measuring body condition

Size-corrected mass is commonly used to determine body condition (Piersma and Davidson 1991, Chastel et al. 1995). Skeletal measurements, such as tarsus and bill length, can be used as a proxy for body size (Kitaysky et al. 1999). Multiple structural measurements provide a more accurate assessment of overall body size than do single measurements (Piersma & Davidson 1991). Principle Components Analysis (PCA) allows a number of measurements from each bird to be combined into a single variable to represent size (Rising & Somers 1989). Rates of primary feather wear can differ among birds and may not be proportional to overall bird size as determined by skeletal measurements (Rising 1988). I found wing chord increased with size as determined by the first principle component of three skeletal measurements: tarsus, head and bill, and culmen ( $R^2 = 0.65$ ,  $p < 0.001$ ). Therefore I used all four structural measurements in a PCA. Principle Component 1 (PC1) explained 80% of the variation among birds. The variables influenced PC1 similarly (loadings 0.48-0.52). As expected, a linear regression showed mass and PC1 were positively related ( $R^2 = 0.77$ ,  $F_{1,81} = 264.3$ ,  $p < 0.001$ ). I used the residuals of mass from the predicted relationship with PC1 (body size) as a measure of body condition.

I used linear regression to analyze differences in body condition and baseline corticosterone levels. I used two-way repeated measures analysis of variance to analyze differences in stress-induced levels of corticosterone between groups of birds.

The four blood samples provided comparisons of corticosterone levels during the capture period for each bird.

#### Other statistical analyses

I used S-PLUS (Version 2000, Mathsoft Inc., Seattle, WA) for most statistical analyses. For the logistic regressions and repeated measures analysis of variance, I used SPSS version 9. I used parametric tests when data met normality assumptions and used non-parametric tests or parametric tests on log-transformed data when data were not normally distributed. I used Welch modified 2-sample t-test for data that were normally distributed but had unequal variances. All Wilcoxon Rank Sum tests and Chi-square tests included continuity corrections. All means are reported  $\pm 1$  standard error. I assumed statistical significance at the 0.05 level.

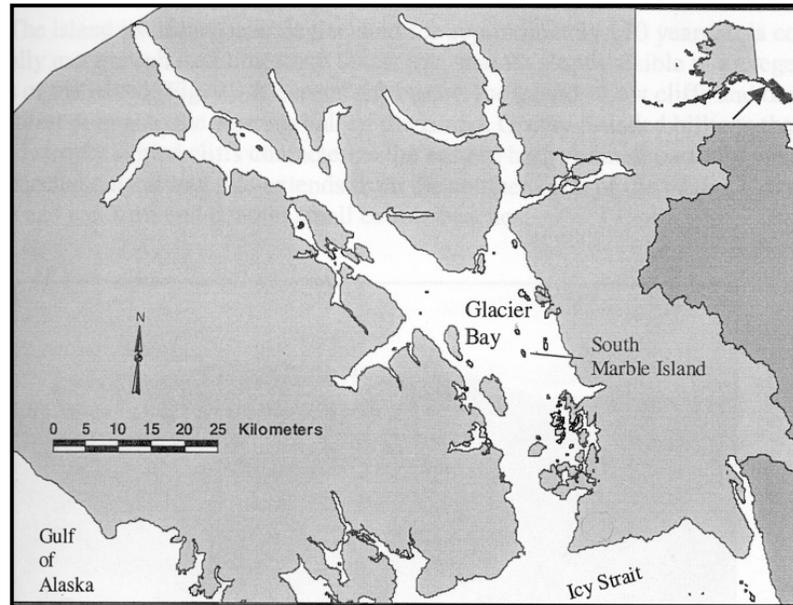


Figure 1. The location of the glaucous-winged gull study colony at South Marble Island.

## RESULTS

## Egg-laying and natural nest predation

Pairs from unmanipulated nests laid clutches of similar sizes each year, but the timing of egg-laying and the total number of eggs laid differed between years. Gulls began laying eggs an average of 6 days earlier in 2000 than in 1999 (Wilcoxon Rank Sum,  $Z = -0.1707$ ,  $p < 0.001$ )(Table 1) and laid significantly more eggs on average in 2000 than in 1999 (Wilcoxon Rank Sum,  $Z = 4.7118$ ,  $p < 0.001$ ). Pairs laid a higher percentage of 3 egg clutches in 2000 (74%) than in 1999 (64%); but these differences only approached significance (Chi-square = 3.25,  $df = 1$ ,  $p = 0.07$ )(Table 2). Many 1 and 2 egg clutches (73% and 50% respectively) were depredated within 5 days of when the last egg was laid. With the depredated nests excluded, the proportion of incomplete clutches (those containing 1 or 2 eggs) did not differ between years (Chi-square = 0.10,  $df = 1$ ,  $p = 0.75$ ).

I observed up to 7 juvenile and adult bald eagles at one time landing at gull nests and eating eggs. I often observed ravens taking black-legged kittiwake eggs and occasionally observed crows picking up small objects within the gull nesting areas, but did not see any direct or indirect evidence of corvid predation on gull eggs. I saw conspecific predation on gull chicks, but never on eggs. I once observed a river otter (*Lutra canadensis*) along the island shore, away from the gull colonies, in the early gull incubation period in 2000. I assume that if corvid, otter, or conspecific predation

occurred, it occurred infrequently and that bald eagles were the primary egg predators of the gulls.

Patterns of eagle predation differed between years. In 1999, I observed adult and juvenile eagles in the gull colonies depredating eggs throughout the incubation period. In 2000, I observed eagles frequently, but did not see many depredated nests until approximately one month after the first gull eggs appeared. Consequently, the timing of nest depredation and re-laying differed between years.

Gulls that re-nested lost their first clutches earlier in the season than those that did not re-nest (1999: Wilcoxon Rank Sum,  $Z = -2.52$ ,  $p = 0.03$ ; 2000: Wilcoxon Rank Sum,  $Z = -2.71$ ,  $p < 0.01$ )(Table 3). The average predation date of clutches that were not replaced was the same in both years (Wilcoxon Rank Sum,  $Z = -0.54$ ,  $p = 0.59$ ), but the average predation date of those that did re-nest was earlier in 1999 than in 2000 (Wilcoxon Rank Sum,  $Z = -2.15$ ,  $p = 0.03$ ). Nests that were depredated early and during their laying cycle resulted in protracted laying. All of these nests contained 1 or 2 eggs at the time of predation.

Because gulls began nesting earlier and the majority of egg predation occurred later, first clutches had been incubated longer when depredated in 2000 than in 1999 (Table 4). This difference occurred between clutches that were subsequently replaced (Wilcoxon Rank Sum.,  $Z = -3.66$ ,  $p < 0.01$ ) and between clutches that were not

replaced (Wilcoxon Rank Sum,  $Z = -4.62$ ,  $p < 0.01$ ). In fact, first clutches that were replaced in 2000 had been incubated longer than clutches that were not replaced in 1999 (Wilcoxon Rank Sum,  $Z = -2.54$ ,  $p = 0.01$ ). Second clutches also tended to be replaced when predation occurred earlier in incubation than in clutches that were not replaced, but my sample sizes were not large enough to test statistically.

### Factors affecting renesting

The variables that were important for predicting whether or not gulls would renest differed between years (Figure 2). Lay date and the age of the clutch at predation were significant factors in the 1999 logistic model ( $-2 \log \text{likelihood} = 58.64$ ). The model correctly predicted 79.25% of the cases ( $X^2_{(2)} = 14.81$ ,  $p < 0.01$ ). The probability of renesting increased with earlier lay dates ( $B = -0.08$ , S.E. 0.04,  $p = 0.03$ ) and younger clutches at the time of predation ( $B = -0.23$ , S.E. = 0.12,  $p = 0.04$ ). The best model for 2000 included the date of predation as the sole factor. The model fit the data ( $-2 \log \text{likelihood} = 82.24$ ) and correctly predicted 69.62% of the cases ( $X^2_{(1)} = 16.38$ ,  $p < 0.01$ ). However, the model had a high rate of false positive predictions that gulls would renest (80%). The probability of renesting increased with earlier predation dates ( $B = -0.14$ , S.E. = 0.05,  $p < 0.01$ ).

### Nest manipulations

*Removing the first egg*

I removed the first egg on the day it was laid in 14 nests in 1999 and 25 nests in 2000. Most (95%) gulls from these nests continued to lay 1 to 3 more eggs (Table 2). Two pairs in 1999 abandoned their nests after the manipulation, but laid replacement clutches 10 and 14 days later. For those pairs that continued to lay, the average number of days before the next egg appeared was significantly longer in 1999 ( $2.45 \pm 0.25$  days) than in 2000 ( $1.80 \pm 0.15$  days) (Wilcoxon Rank Sum,  $Z = 2.0818$ ,  $p = 0.0374$ ). Following egg removal, 46% of pairs laid the remainder of their clutches in new nest structures built an average of  $2.20 \pm 0.42$ m ( $n = 15$  nests) from their original structures, presumably within the same defended territory.

Gulls completed a clutch of 3 by laying a fourth egg in 78% of the manipulated nests (Table 2). The proportion of pairs that laid only 1 or 2 more eggs following loss of the first did not differ from the proportion of unmanipulated birds that laid 1 and 2 egg clutches whether the unmanipulated nests that were depredated during the laying sequence were included ( $X^2_{(1)} = 1.05$ ,  $p = 0.30$ ) or excluded from the analyses ( $X^2_{(1)} = 0.37$ ,  $p$ -value = 0.54).

Pairs with their first egg removed laid on average 1.24 (in 1999) and 1.06 (in 2000) more eggs than those in the unmanipulated group, but there was no difference in the number of eggs that hatched in either year (1999: Wilcoxon Rank Sum,  $Z = 0.24$ ,  $p = 0.81$ ; 2000:  $Z = 1.05$ ,  $p = 0.29$ ) (Table 2). The total number of eggs laid at the

manipulated nests did not differ between the years (Wilcoxon Rank Sum,  $Z = -1.22$ ,  $p = 0.22$ ).

### *Removing the clutch*

I removed the clutch on the day the third egg was laid in 17 nests in 1999 and 24 nests in 2000. In 1999, the median lay date of the first egg in nests from which I removed the clutch was earlier than in the unmanipulated nests (Wilcoxon Rank Sum,  $Z = -2.567$ ,  $p = 0.0103$ ), but not in 2000 (Wilcoxon Rank Sum,  $Z = -1.7301$ ,  $p = 0.0836$ ) (Table 1). Most (93%) gulls from these nests laid replacement clutches of 1 to 3 eggs (Table 2). I did not find replacement clutches for 1 pair in 1999 and 2 pairs in 2000, and I presume that those pairs did not re-nest. The number of days between the clutch removal and the lay date of the first egg of the second clutch did not differ between years (Wilcoxon Rank Sum,  $Z = 1.46$ ,  $p = 0.14$ ). Pairs laid their second clutches in new nests an average of  $2.19 \pm 0.31$  m ( $n = 28$  nests) from their first nests. These distances were not significantly different from the distances between successive nests in the first egg-removed group ( $F = 0.10$ ,  $df = 1$ ,  $p = 0.75$ ).

Pairs replaced their clutches with another 3-egg clutch in 82% of the cases (Table 2). In 2000, 2 nests were depredated within 2 days of when the first and second eggs were laid, so I do not know what the final clutch size would have been if predation had not occurred. The proportion of replacement clutches that contained 3 eggs did not differ from the proportion of unmanipulated clutches that contained 3 eggs ( $X^2_{(1)} = 2.11$ ,  $p =$

0.15). This pattern remained the same when depredated nests were excluded from the analyses ( $X^2_{(1)} = 0.01$ ,  $p = 0.93$ ).

The numbers of eggs laid at the manipulated nests did not differ between years (Wilcoxon Rank Sum,  $Z = 0.51$ ,  $p = 0.61$ ) (Table 2). Pairs with their clutches removed laid on average 2.71 (in 1999) and 2.01 (in 2000) more eggs than those in the unmanipulated group, but there was no difference in the number of eggs that hatched in either year (1999: Wilcoxon Rank Sum,  $Z = 1.15$ ,  $p = 0.25$ ; 2000:  $Z = -0.26$ ,  $p = 0.79$ ).

#### Physiological effects of laying replacement eggs

##### *Body condition*

Body condition of gulls that had fully incubated their original clutch or a replacement clutch did not differ by capture date ( $F = 0.03$ ,  $df = 1, 41$ ,  $p = 0.85$ ), sex ( $F = 0.59$ ,  $df = 1, 41$ ,  $p = 0.45$ ), year ( $F = 0.33$ ,  $df = 1, 41$ ,  $p = 0.57$ ), or treatment ( $F = 0.29$ ,  $df = 1, 41$ ,  $p = 0.59$ ). None of the interaction terms in the saturated model were significant. There was a weak relationship between volume of the first egg and lay date in 1999 ( $R^2 = 0.06$ ,  $F = 6.09$ ,  $df = 1, 103$ ,  $p = 0.02$ ) and no relationship in 2000 ( $R^2 < 0.01$ ,  $F = 0.34$ ,  $df = 1, 160$ ,  $p = 0.59$ ). In females, body condition did not vary with lay date or the average volume of the first and second eggs in either the replacement clutch group ( $R^2$

= 0.61,  $F = 1.56$ ,  $df = 3,3$ ,  $p = 0.36$ ) or original clutch group ( $R^2 = 0.14$ ,  $F = 1.56$ ,  $df = 3,10$ ,  $p = 0.70$ ).

#### *Baseline corticosterone*

Baseline levels of corticosterone in gulls that had fully incubated their original clutch or a replacement clutch did not vary by the date of capture (Males:  $R^2 = 0.03$ ,  $F = 0.23$ ,  $df = 1,7$ ,  $p = 0.64$ ; Females:  $R^2 < 0.01$ ,  $F = 0.05$ ,  $df = 1,14$ ,  $p = 0.82$ ). Average baseline levels were  $8.39 \pm 1.62$  ng/ml ( $n = 9$ ) in males and  $6.98 \pm 0.94$  ng/ml ( $n = 16$ ) in females. However, baseline levels in females from control nests were higher in 2000 than in 1999 ( $t = -2.34$ ,  $df = 9$ ,  $p < 0.01$ , power = 1.0). I was able to test females for differences between treatments in 2000 only and found that levels did not differ ( $t = 0.75$ ,  $df = 8$ ,  $p = 0.476$ , power = 0.98). I found no differences in males between years ( $t = 0.55$ ,  $df = 7$ ,  $p = 0.60$ , power = 0.95) or treatments ( $t = 0.12$ ,  $df = 7$ ,  $p = 0.91$ , power = 0.92).

#### *Stress-induced corticosterone*

Females responded to being captured by a significant increase in corticosterone levels (time after capture: 116.81,  $df = 3,33$ ,  $p < 0.01$ )(Figure 3). Although mean stress-induced levels were not significantly different between gulls that had fully incubated their original clutch or a replacement ( $F = 1.85$ ,  $df = 1,11$ ,  $p = 0.20$ ), the rate of increase was significantly different (time after capture \* treatment interaction term:  $F$

= 5.97,  $df = 3,33$ ,  $p < 0.01$ ). Females that replaced a clutch secreted lower maximum levels of corticosterone than those that incubated their original clutch ( $F = 7.96$ ,  $df = 1,7$ ,  $p = 0.03$ ). Males also responded to being captured by a significant increase in corticosterone levels (time after capture:  $F = 80.38$ ,  $df = 3,21$ ,  $p < 0.01$ ). I combined years to increase our sample size because year had no effect on either the mean stress-induced levels ( $F = 1.10$ ,  $df = 1,7$ ,  $p = 0.33$ ) or the rate of increase (time after capture \* year interaction term:  $F = 0.82$ ,  $df = 3,21$ ,  $p = 0.50$ ). Whether males incubated a replacement or original clutch did not significantly affect their mean stress-induced levels ( $F = 0.18$ ,  $df = 1,7$ ,  $p = 0.69$ ) or the rate of increase (time after capture \* treatment:  $F = 0.61$ ,  $df = 3,21$ ,  $p = 0.62$ ).

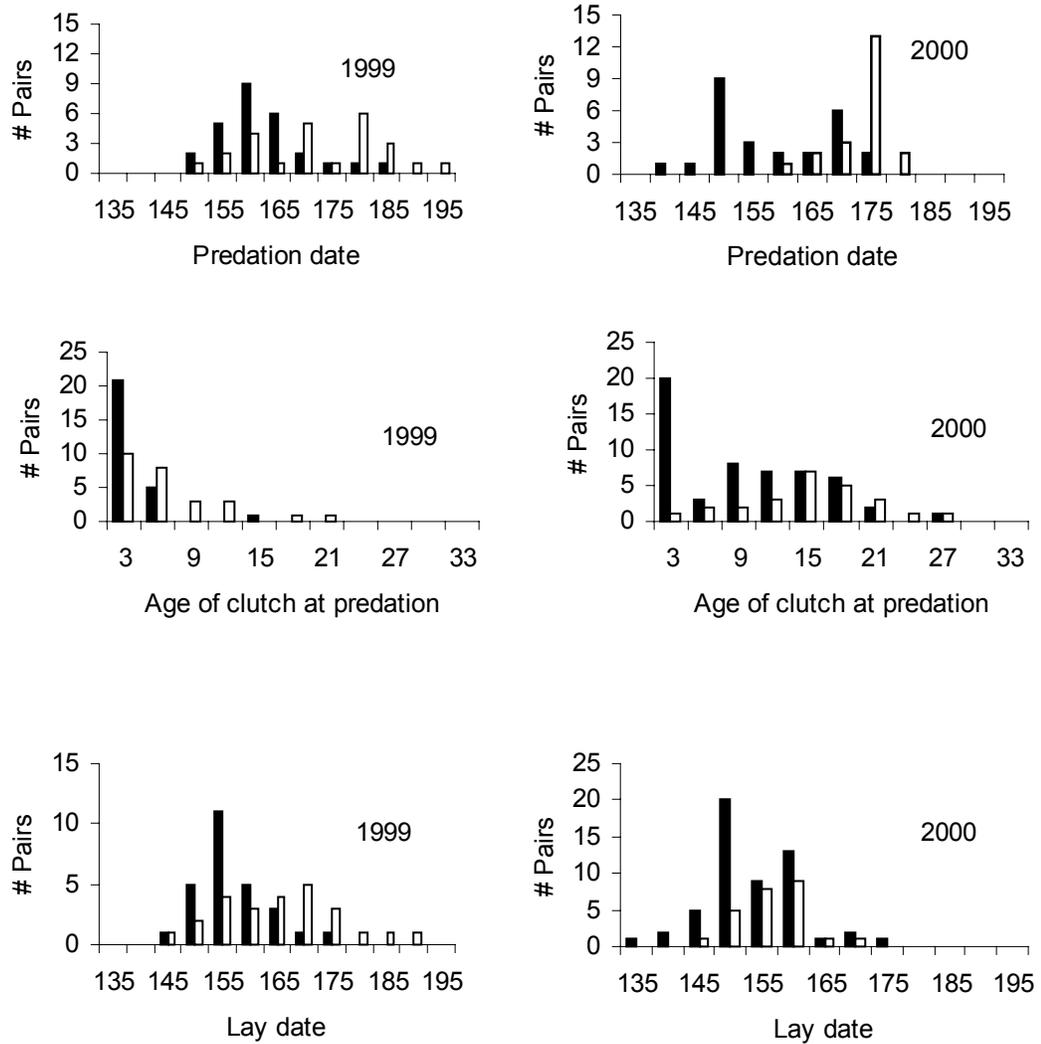


Figure 2. Histograms of the number of pairs that relaid (black) and did not relaid (white) after losing their first clutches to predation as a function of the date of predation, the age of the clutch at predation and the lay date of the first egg in the clutch.

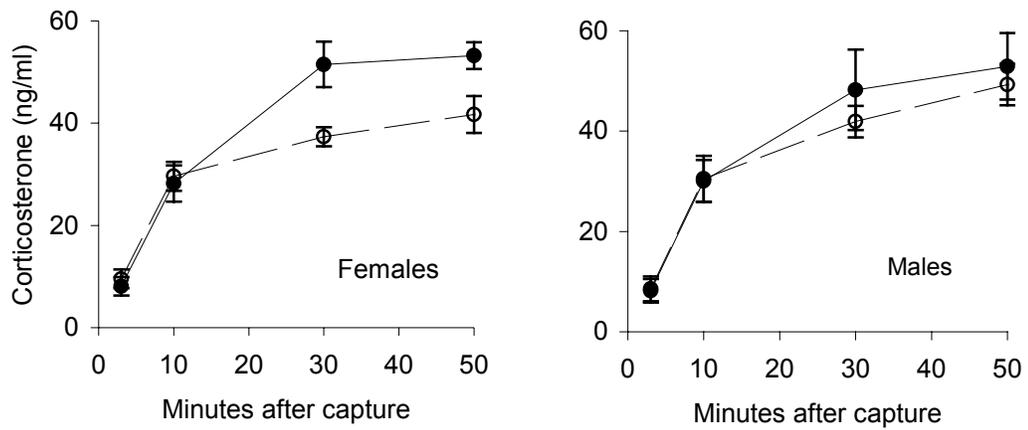


Figure 3. Stress-induced levels of corticosterone in gulls captured at the end of their incubation effort. Gulls at nests with original clutches (solid line; N = 5 in each sex) are compared with gulls at nests with replacement clutches (dashed line; N = 4 in each sex).

Table 1. Phenology and productivity at experimental and unmanipulated nests. Mean and median lay dates include only those nests for which the exact lay date of the first egg is known. Numbers of eggs laid include those lost to natural predation.

Treatment	N	<u>Lay date of first egg</u>		<u>Eggs laid</u>		<u>Eggs hatched</u>	
		Mean	Median	Mean	Mode	Mean	Mode
<u>1<sup>st</sup> egg removed</u>							
1999	14	June 7 ± 0.82 days	June 8	4.29 ± 0.32	4	1.71 ± 0.40	3
2000	25	May 28 ± 0.44 days	May 28	4.80 ± 0.28	4	1.92 ± 0.24	3
<u>Clutch removed</u>							
1999	17	June 2 ± 0.44 days <sup>1</sup>	June 2 <sup>1</sup>	5.76 ± 0.20	6	2.00 ± 0.33	3
2000	24	May 29 ± 0.40 days <sup>3</sup>	May 29	5.75 ± 0.25	6	1.67 ± 0.27	3
<u>Unmanipulated</u>							
1999	151	June 8 ± 0.76 days <sup>2</sup>	June 5 <sup>2</sup>	3.05 ± 0.09	3	1.61 ± 0.11	3
2000	140	June 2 ± 0.83 days <sup>4</sup>	May 30	3.74 ± 0.12	3	1.81 ± 0.11	3

<sup>1</sup> N = 9 nests

<sup>2</sup> N = 87 nests

<sup>3</sup> N = 22 nests

<sup>4</sup> N = 115 nests

Table 2. Direct results of glaucous-winged gull nest manipulations in 1999 and 2000. Differences between years where  $p < 0.01$  are indicated by bold face type.

Treatment	N	Continued to lay	Interval (days)	Switched nests	Laid 3 eggs	Laid 2 eggs	Laid 1 egg
1 <sup>st</sup> egg removed	39	37(95%)	<b>2.06 ±</b> <b>0.14<sup>1</sup></b>	17(46%)	29(78%)	7(18%)	1(3%)
Clutch removed	41	38(93%)	12.18 ± 0.28	31(82%)	31(82%)	5(13%) <sup>2</sup>	2(5%) <sup>3</sup>
Unmanipulated	291 <sup>4</sup>				199(68%)	58(20%) <sup>5</sup>	33(11%) <sup>6</sup>

<sup>1</sup> N = 36; one interval not known and not included

<sup>2</sup> One nest depredated within 2 days of when the second egg was laid.

<sup>3</sup> Depredated within 2 days.

<sup>4</sup> Includes 1 clutch with 4 eggs

<sup>5</sup> 29 nests depredated when the last-laid egg had been in the nest  $\leq 5$  days

<sup>6</sup> 24 nests depredated when the last-laid egg had been in the nest  $\leq 5$  days

Table 3. Average dates of predation events of unmanipulated glaucous-winged gull nests.

		Date of nest predation of first nesting attempt		
		Caused protracted laying	Re-nested	Did not re-nest
1999	June 6 ± 1.70 (9)	June 13 ± 1.10 days (18)	June 20 ± 2.24 days (26)	
2000	June 1 ± 2.73 (11)	June 15 ± 1.39 days (43)	June 21 ± 1.29 days (25)	

Table 4. Average clutch age (in days) of depredated glaucous-winged gull nests. All clutches are from first nesting attempts in unmanipulated nests. Nests in which protracted laying followed predation are not included.

	N	# Clutches depredated <sup>1</sup>	Clutch age at predation	
			Re-nested	Did not re-nest
1999	151	53 (35%)	3.39 ± 0.75 (34%)	5.88 ± 0.92 (49%)
2000	140	79 (56%) <sup>3</sup>	9.88 ± 0.95 (54%)	14.24 ± 1.08 (32%)

<sup>3</sup> Includes 6 that disappeared with no evidence of predation

## DISCUSSION

The high natural predation pressure the gulls experience and their resulting re-nesting patterns varied annually at South Marble Island. Ultimately, hatching success remained unchanged by either natural predation or my experimental egg-removals. However, individual physiological measurements were sensitive to showing proximate effects of replacing a clutch.

### Natural nest predation and renesting

Bald eagles in Washington State have caused egg loss in glaucous-winged gulls directly by eating eggs (Good et al. 2000; Thompson 1989) and indirectly by flushing parent gulls, thereby facilitating egg predation by conspecifics (Good et al. 2000). Verbeek (1982) found more double-crested (*Phalacrocorax auritus*) and pelagic cormorant (*P. pelagicus*) eggs depredated by American crows on days when bald eagles were present. Ewins (1991) proposed that trees close to the gull colony facilitated corvid predation by affording protection to the corvids from gull attacks. The forest on South Marble Island appears to facilitate eagle predation similarly. Juvenile and adult eagles often roosted in the trees, periodically flying into the gull colonies and returning to the trees after successful and unsuccessful forays. Gulls often mobbed the eagles in the air, but usually stopped when the eagles landed in the trees.

Individual bird quality can influence decisions to relay after egg loss (Wendeln et al. 2000). High parental quality in larids has been attributed to age (i.e., breeding experience), early laying, and laying large eggs. The influence of these factors is often difficult to separate. Early nesting red-billed gulls (*Novaehollandiae scopulinus*) were considered higher quality because the mean egg sizes of early nesting pairs, that lost a clutch and relayed, were larger than those of birds laying first clutches at the same time (Mills 1979). Egg size in western gulls (*Larus occidentalis*) was positively influenced by female physiological condition and possibly food availability (Pierotti & Bellrose 1986). The mean egg mass in the first clutch of common terns that relaid did not differ from those that did not relay (Wendeln et al. 2000). However, older common terns laid earlier and were more likely to relay after egg removal than younger terns (Wendeln et al. 2000).

In this study, the factors in the logistic models which best predicted whether or not gulls at the unmanipulated nests would lay replacement eggs support the idea that renesting patterns are variable in response to predation patterns. Because predation rates were more constant in 1999, nests were attacked as they appeared. Lay date and the age of clutch at predation, both potentially related to parental quality, were significant variables in predicting whether birds renested. In 2000, the effect of parental quality may have been obscured by the synchrony of predation. The confounding influences of nesting early, generally positively associated with renesting, and losing clutches late, generally negatively associated with renesting, may

have decreased the parental quality advantage. The high percentage of false positive predictions of the otherwise strong logistic model supports this idea. Losing clutches late in that year discouraged renesting in both early and late nesters. Because breeding began earlier, losing clutches earlier did not necessarily lead to renesting because those clutches had been incubated longer.

#### Experimental egg-removal

I was able to induce replacement laying for eggs taken during and after the egg-laying sequence without affecting mean hatching success. Egg laying after egg removal can be considered complete replacement laying if the total number of eggs laid is the sum of the number originally intended and the number removed. Originally intended clutch size is impossible to know at an individual level, but may be inferred at a population level. I found that when including the effects of natural predation, the birds from which I removed their first egg were able to completely replace this egg by laying on average at least one more egg than the unmanipulated group. In contrast, the population from which I removed the clutch of three was less likely to do so. These data suggest that it is more difficult to get complete replacement laying on a population level as the number of eggs taken increases.

The number of days between (1) the removal of the first egg and the appearance of the second egg and (2) the removal of the clutch and the appearance of the first egg of the

replacement clutch were similar to what has been recorded for glaucous-winged gulls (Verbeek 1993). The differences I saw between years in the interval between the first removed egg and the second egg may have resulted from the greater variability in the time of day of our nest checks in 1999. Gulls lay throughout the day, with a possible higher frequency in the first hour after sunrise (Verbeek 1993), so our more regularly timed nest checks in 2000 may have minimized variability. Influences on relaying intervals can vary between species. In herring gulls, seasonal effects were found to be greater than clutch-age effects on the days to lay replacement clutches (Parsons 1976); whereas in common terns, clutch age, but not season, was related to relaying interval. (Wooler 1980). I likely did not find differences because our study minimized clutch age and seasonal effects by controlling the timing of egg-removal.

The loss of the first egg during the egg-laying sequence did not keep most pairs from abandoning further laying attempts. Two pairs from which I removed their first egg responded as if they lost a clutch by laying replacement eggs 10-14 days later. These may have been 1-egg clutches, similar to the 4% of the unmanipulated clutches composed of 1 egg. The percentage of gulls at South Marble that laid fourth eggs to replace the first egg (78%) is similar to that reported for early nesting herring gulls under the same treatment. Parsons (1976) reported 59% of herring gulls with first eggs removed laid a fourth egg, but the ability to lay a fourth egg declined from 79% early in the season to 48% later.

Higher percentages of gulls (93%) from which I removed clutches replaced them than have been reported for other larids and for the unmanipulated gulls that lost eggs to natural predation during our study. Black-legged kittiwakes replaced 32% of 19 lost clutches (Maunder and Threlfall 1972). Black-headed gulls (*Larus ridibundus*) replaced 32% of 25 clutches that were removed (Weidmann 1956). Herring gulls replaced 70% of 84 clutches that were removed within four days of the lay date of the last egg (Parsons 1976). These differences may in part be explained by the controlled timing of our egg-removal. Parsons (1976) found the clutch age and the lay date to negatively correlate with the likelihood of relaying in herring gulls, but was not able to distinguish the effects of the two factors. Our removal method standardized the clutch age at loss to less than 24 hours, which may have maximized the reneesting rates. The gulls in our study may also respond differently to the loss of their eggs by our removal and by eagle predation, but I was unable to test for these effects.

I found that the gulls often laid eggs in new nest structures following the loss of their original egg(s). About half (38-57%) of control clutches lost to natural predation were replaced in new nest structures. The values were within the range I saw at the nests I manipulated. In those nests, gulls that lost complete clutches switched more often (63-91%) than those that lost a single egg during the laying phase (44-50%). Switching nests after the loss of eggs may be common strategy in many larids. In Washington State, 27% of glaucous-winged gulls that had eggs experimentally removed continued to lay in different nests (Reid 1988). In common terns, 89% laid second clutches in

new nests (Wendeln et al. 2000), while 86% that had the first egg experimentally removed continued to lay in a second nest (Arnold et al. 1998). Laying replacement eggs in a nest that has been exposed to predation may increase vulnerability of the nest to more predation. However, laying replacement eggs in new nests that were still in the same territories did not prevent further fox predation in two gull species (Shugart & Scharf 1977; Southern et al. 1985).

### Physiological effects

The two groups I analyzed for physiological effects of relaying eggs were successful breeders; individuals from both had incubated to hatching full clutches of three eggs, either an original or replacement clutch. Wendeln (2000) posits that if birds that renest are high quality, the extra effort may not affect them. I did not know the age of the breeding birds in this study, which can reflect bird quality, nor did I find strong relationships between egg volume and lay date, which can also reflect bird quality. However, I found evidence of some physiological response to renesting that would not have been seen in the more common measures of bird quality such as body condition and hatching success.

The baseline corticosterone level and body condition of the gulls in our experiment suggest that the birds were not undergoing chronic stress. Studies have shown that baseline corticosterone levels vary seasonally, increasing at highest rates at colonies

with unfavorable environmental conditions (Kitaysky et al. 1999). I controlled for the effects of progressive reproductive stages on corticosterone by sampling individuals at the end of their incubation. Seasonal effects, as measured by the sampling date, had no effect on baseline corticosterone. Levels were within what is considered to be representative of non-stressed glaucous-winged gulls (A. Edwards, unpublished data). As poor body condition has been found to be associated with elevated baseline levels (A. Edwards, unpublished data) and I found no trends in body condition, I can presume the birds in our study comprised healthy individuals.

However, I found evidence of stress response modulation in females that had laid 3 additional eggs. Stress responses in black-legged kittiwakes increase as the breeding season progresses and concomitant parental energetic demands increase (Kitaysky et al. 1999). Our expectation is that the stress response in the gulls on South Marble would also increase as individuals progressed through their breeding stages. However, I restricted our sampling to birds at the end of their incubation; the difference between the groups was therefore the energetic investment to that point. Males and females from nests with replacement clutches both increased the investment to complete incubation when compared with birds incubating their original clutches. However, I saw suppression only in females, which suggests that the process of producing the additional 3 eggs, whether or not in combination with the greater time investment, disproportionately affected females.

Suppressing responses to acute stress may be evolutionarily advantageous to female gulls. Suppressed stress responses have been seen in passerine birds breeding under severe environmental conditions compared with conspecifics breeding in less severe environments (Wingfield et al. 1995). As stress responses facilitate behaviors such as abandonment of reproduction, suppression of this response allows the birds to continue breeding under unfavorable conditions (Wingfield et al. 1995). Kitaysky *et al.* (1999) found stress response suppression in kittiwakes breeding during food shortages. The authors suggested that the suppression could offer evolutionary advantages by allowing successful breeding over abandonment of breeding effort, which would fit the prediction of the life-history trade-off between body maintenance and reproductive processes in long-lived animals. Although I saw no decrease in body condition in the female gulls that had incubated replacement clutches when compared with control females, the additional energetic demands resulting from laying a replacement clutch could have increased the likelihood of abandonment when faced with potential stressors. Suppression of this response may have allowed the females to continue incubating, thereby not reducing their hatching success.

Although hatching success was similar between groups, there may be future effects on the resulting chicks beyond the scope of the study. Daan (1986) describes a pattern of declining fledgling success and post-fledging survival as a function of laying and hatching dates. This pattern has been observed in larids. Due to the time required to lay replacement eggs, chick-hatching dates are necessarily delayed. Hatching late led

to lower survival rates for glaucous-winged gull chicks in a year of poor food availability, but the relationship was not strong when food supply was high (Hunt & Hunt 1976). Herring gulls hatched from replacement clutches have been found to suffer higher post-fledging mortality (Nisbet & Drury 1972). Hatching late was found not to affect post-fledging survival in common terns (Nisbet 1996, Becker 1999). However, in black-headed gulls, chicks that hatched late began breeding at an older age (Prevot-Julliard et al. 2000).

#### Future impacts of egg-harvesting

Egg removal by humans has been shown to effect population declines in gulls. In one management project which removed herring gull eggs every 1-3 weeks over the course of 3 consecutive breeding seasons, the gull population continued to nest, but the maximum number of nests during a visit declined 67%. At a second colony, removing eggs at 1-week intervals for 2 consecutive breeding seasons caused a 57% reduction in the maximum number of eggs (Ickes et al. 1998). No chicks were produced at a glaucous-winged gull colony in British Columbia where egg collecting had occurred throughout the laying and incubation period (Vermeer et al. 1991). Biweekly nest and egg destruction at a herring and great black-backed (*Larus marinus*) gull colony prevented any fledging (Olinjynk & Brown 1999). After 3 years of this treatment, the number of nesting attempts declined 60%. Response to egg removal can vary by species. Intensive egg removals from herring and lesser black-backed gulls appeared

more successful at controlling the herring gull population than the black-backed gull population (Wanless et al. 1996).

Natural variability is a useful reference when setting management goals (Landres et al. 1999). It is important to consider variability when searching for a suitable management strategy that allows egg harvesting without negatively affecting the population dynamics of the gull colony. Even in this study, I found annual variability in breeding phenology, predation pressure, and the response of the gulls to predation. In addition, my study supports the idea that individual bird quality can influence responses to egg predation, and that even high quality breeders may show effects of laying replacement eggs. Although ecological research can aid managers in designing management programs, such programs will entail risks (Hilborn & Ludwig 1993). The long-term effects of natural predation and reneating at the individual and the population level of gulls in Glacier Bay are unknown at this point and deserve further study. An adaptive management program that incorporates measures of and responses to natural variability may be the most prudent choice.

### Management guidelines

The goal of Glacier Bay National Park is to allow egg harvesting without negatively impacting the population dynamics of the gull colony at South Marble Island (M. B. Moss, pers.comm.). The results of my studies suggest that limited egg harvesting can

fit within that management goal. Analyses of natural predation and experiment removals suggest that gulls will replace eggs if they are taken early (by mid-June) without decreasing their hatching success. Due to the high disturbance human presence causes when chicks are present, access to the nesting areas should be restricted when the first chick hatches (Robert & Ralph 1975). Because the loss of eggs in the nest causes either protracted laying (if the clutch has not yet been completed) or replacement laying (if the clutch has been completed), removing the entire contents of a nest would likely initiate further laying. In contrast, removing only part of a completed clutch in the nest would likely not trigger re-laying. In the first scenario, gulls may lay more eggs in total, but chick survival may be reduced. In the second scenario, the number of chicks that hatched would be reduced, but chick survival may be higher. Because many of the longer-term impacts of egg harvesting are unknown, I believe shifting harvesting locations each year would reduce the overall impact on the colony. However, harvesting locations should be chosen to minimize disturbance to other species nesting on the island.

An annual monitoring program should be implemented immediately. This program should include an annual census of adult gulls visible to observers circumnavigating the island during the period of mid-incubation. This information would provide the simplest, albeit coarse, method of monitoring the population size over time. Early in the breeding season (before and during egg-laying) observers should search for adults that were color-banded during the course of this study. This information would be

valuable for determining adult survivorship rates. Counts of bald eagles seen at the island during the course of the summer would provide information of the duration and intensity of natural egg-predation. It is also important to consider that the forest may eventually displace the gulls on South Marble Island regardless of variations in predation rates. Quantification and monitoring of the vegetation succession on the island will provide a longer-term view of the potential trends of the gull colony.

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Appendix A. Results of removing the first egg from a nest on the day it was laid in 1999.

Switched nests after manipulation (Yes, No)	Days to lay next egg	# eggs laid	Clutch age at predation	Switched nests	Days to lay next egg	# eggs laid	Clutch age at predation	Fate	Total nests us
Y	3	3						3H	2
Y	4	3						3H	2
Y	14	3						3E	2
N	2	3						3H	1
N	2	3	21					No re-lay?	
Y	3	3	0 <sup>1</sup>	N	12	3	18	2E	2
N	1	2						2H	1
N	11	1	0	N	2	1	2	2H <sup>2</sup>	1
N	3	3	5	Y	11	3		3E	2
N	2	3						3H	1
Y	<5	3						1U (H?), 2F	2
Y	2	2						2H	2
Y	3	3						3H	2
N	2	3						3H	1

<sup>1</sup> We took the clutch on the day the third egg was laid

<sup>2</sup> 2 eggs laid 1 and 3 days later; both hatched

Appendix B. Results of removing the first egg from a nest on the day it was laid in 2000.

Switched nests after manipulation (Yes, No)	Days to lay next egg	# eggs laid	Clutch age at predation	Switched nests	Days to lay next egg	# eggs laid	Clutch age at predation	Fate	Total ne used
N	3	3	13	N	15	3	-	3H	
N	3	3	11	N	18	3	-	2H,1F	
N	1	3	14	Y	11	3	-	2H,1F	
N	2	3	3	Y	11	3	-	3H	
N	2	3	4	Y	12	3	-	3H	
N	3	3	14	Y	12	3	-	2H,1SF	
N	1	3	15	Y	15	2	-	1H,1PE	
Y	2	1	10	Y	5	3	-	2H,1SF	
Y	3	2	18	Y	11	2	-	1H,1F	
Y	1	2	24	Y	13	2	12	No re-lay	
N	2	3	23	-				No re-lay	
Y	1	3	12	-				No re-lay	
Y	2	3	21	-				No re-lay	
Y	2	3	17	-				No re-lay	
N	1	2	-					2H	
N	1	3	-					3H	
N	2	3	-					1PE,2SF	
N	1	3	-					3H	
N	1	3	-					3H	
N	1	2	-					2H	
Y	2	3	-					2H,1PE	
Y	3	3	-					3H	
Y	3	2	-					2H	
Y	1	3	-					2H,1F	
Y	3	3	-					3F	

Appendix C. Results of removing the clutch from a nest on the day the third egg was laid in 1999.

Switched nests after manipulation (Yes, No)	Days to lay next egg	# eggs laid	Clutch age at predation	Switched nests	Days to lay next egg	# eggs laid	Fate	Total nests used
Y	12	3					3H	2
Y	14	2					2E	2
N	12	3	10	Y	9	1	No re-lay? <sup>1</sup>	2
Y	11	3					3SF	2
Y	13	3					2SF,1E	2
Y	10	3					2H,1PE	2
Y	12	3					2H,1PE	2
N	11	3					2H,1PE	1
Y	12	3					2H,1PE	2
N	15	3					2PE,1SF	1
Y	14	3					1H,1PE,1SF	2
N	12	3					2H,1SF	1
Y	12	3					1PE,1SF,1E	2
N	13	3	4				No re-lay?	
Y	14	3					1H,2PE	2
No re-lay?								
Y	12	1	0	Y	3	1	No re-lay <sup>2</sup>	3

<sup>1</sup> Egg disappeared at day 11; no following replacement attempt

<sup>2</sup> Last egg depredated on lay date; no following replacement attempt

Appendix D. Results of removing the clutch from a nest on the day the third egg was laid in 2000.

Switched nests after manipulation	Days to lay next egg	# eggs laid	Clutch age at predation	Switched nests	Days to lay next egg	# eggs laid	Fate	Total nests used
N	11	3					1F <sup>1</sup>	1
N	20	3					2H <sup>2</sup>	1
Y	12	1	2	Y	2	1	1H	2
Y	12	3	1	Y	12	2	1H <sup>3</sup>	3
Y	11	3	6	Y	13	3	3E <sup>4</sup>	3
Y	13	2	4				No re-lay	2
Y	11	3	5				No re-lay	2
Y	11	2	11				No re-lay	2
Y	12	3	6,14				No re-lay	2
Y	13	2					2F	2
Y	11	3					2H <sup>5</sup>	2
Y	11	2					2H	2
Y	12	3					3H	2
Y	11	3					3H	2
Y	12	3					3H	2
Y	12	3					3H	2
Y	11	3					2H,1PE	2
Y	11	3					1H,2SF	2
Y	12	3					3H	2
Y	10	3					1H,1F <sup>6</sup>	2
Y	12	3					3H	2
Y	12	3					3H	2
No re-lay								1?
No re-lay								1?

<sup>1</sup> One egg depredated at 10 days; one egg disappeared at 30 days and may have hatched.

<sup>2</sup> One egg disappeared at 5 days.

<sup>3</sup> 1 egg in nest at day 23 when last observed

<sup>4</sup> We observed the eggs until day 30, when we left the island and did not see if they hatched.

<sup>5</sup> One egg disappeared at 14 days.

<sup>6</sup> One egg disappeared at 12 days.